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FINAL REPORT

Effects of Background Gravity Stimuli
on Gravity-Controlled Behavior

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I. Introduction & Rationale

The advent of space flight has triggered a considerable amount of research on the physiological and developmental effects of altered gravity. (e.g., Wunder, 1966; Oyama, 1965). Notably fewer experiments have dealt with the effects of gravity or changes in gravity upon behavioral processes. Many of the behavioral experiments which have been reported however, have viewed gravity as an interference factor which affects ongoing performance. (e.g., Beasley and Seldean, 1965; Riccio and Thach, 1966).

As a result of NASA funding to the University of Kentucky, a more fundamental approach has been adopted. This view focuses upon the stimulus properties of gravity. More specifically, gravity is seen as a stimulus dimension which, like more familiar dimensions (e.g. light, sound), can be shown to control behavior. In addition to discriminative properties, gravitational stimuli have been found to possess reinforcing and aversive properties.

Three basic experimental approaches have been taken. In the first, animals are placed into fields of artificial gravity in the form of parabolic or spiral centrifuges. The subjects can effect changes in gravity by locomoting inward or outward along the track, changing radius. A "gravity preference" is inferred when an animal spends a predominant amount of time in one gravity region. These laboratory experiments unequivocally demonstrate that several species of animal select the lowest gravity available, 1.0 g (Lange and Broderson, 1965; Broderson and Lange, 1969). A more recent experiment showed that rats chronically

centrifuged in excess of 2.0 g for a period of one year initially manifested a marked preference for 2.0 g which was later replaced by a moderate preference for 1.0 g (McCoy and Jankovich, 1972). This experiment demonstrates that gravity preference is modifiable and is a function of the "background" or "reference" gravity level.

A second type of experiment capitalizes on the increased precision and reliability afforded through operant conditioning techniques. In this paradigm, an experimental chamber containing a lever is located on the centrifuge. Lever presses reduce gravity or postpone programmed increases. These studies demonstrate that gravity in excess of earth gravity is aversive (Martin, Richardson and Martin, 1966) and that rats and primates will acquire responses which escape high gravity or postpone gravity increases (Clark, Martin, Lange and Belleville, 1969; McCoy, Love and Roberts, 1969).

Still other procedures involve discrimination and generalization of gravitational stimuli (McCoy and Lange, 1969). Animals trained to emit lever responses at one gravity value show gradients of responding to neighboring values with response rate decreasing as the test stimuli depart from the training stimulus. Stimulus control is enhanced when gravity discriminations are required and generalization gradients of gravity exhibit many of the properties of more conventional stimuli (e.g., peak shift, Hanson, 1959). Moreover, the generalization technique has been used to establish that artificial gravity, and not rotation, is the controlling stimulus in these experiments. (McCoy, Love & Miller, 1971).

Taken together, these findings point to the present need for a viable experimental program which utilizes this knowledge as a foundation

for the development of a psychophysics of gravity on the one hand, and on the other hand, explores and delineates the background factors which support these behaviors. It was to these issues that the present grant was directed.

II. Gravity Preference

A host of experiments has demonstrated that normal earth-raised rats, when placed in fields of centrifugally-produced artificial gravity, will select the lowest gravity possible, 1.0 g (e.g., Lange & Broderson, 1965; Broderson & Lange, 1969).

Each of the experiments contained one logical flaw; viz it was not clear whether animals preferred the lowest gravity possible, or the g magnitude most often experienced. In both cases, it was 1.0 g. This confounding could be alleviated by extending the range of gravity field to some region below 1.0 g. Under such circumstances, a preference for 1.0 g would support the idea that normally reared animals prefer that gravity most similar to Earth gravity. The selection of a gravity field below 1.0 g would strengthen the contention that, within limits, animals prefer the lowest gravity available. However, such experiments are impractical because they require orbital inflight experiments in order to obtain gravities below 1.0 g for protracted periods of time. Although suborbital experiments have been attempted (Lange & Belleville, 1971), they are too brief to draw definite conclusions.

An alternative approach, and the one adopted under this grant, was to maintain animals at gravities higher than earth gravity for prolonged

periods of time. The animals were then given gravity preference tests in spiral centrifuges which ranged from 1.0 g to 2.0+ g. Such a design enables one to evaluate whether the mechanism underlying gravity preference is one of familiarity. That is, if animals prefer the most familiar gravity environment, then chronically centrifuged subjects should select some gravity range other than 1.0 g, presumably near that level at which they have been previously exposed.

The prototype experiment was conducted by McCoy & Jankovich (1972). Rats were chronically centrifuged in excess of 2.0 g for 6 or 12 months. They were then given four 24-hour gravity preference tests in a spiral centrifuge in which they could adjust the gravity level imposed by locomoting inward or outward radially along a track. Chronically centrifuged rats spent as much time at 2.0 g as at 1.0 g while normally raised controls selected 1.0 g exclusively. Further analysis of the performance of the chronically centrifuged animals revealed that the initial preference for 2.0 g was replaced by a preference for 1.0 g. These results indicate that hypergravity is not necessarily an aversive stimulus and that gravity preference behavior may depend upon the initial "reference level" involved. The ultimate selection of 1.0 g by chronically centrifuged animals suggests that a preference for a familiar gravity environment may be replaced by a preference for low gravity stimuli.

During the grant period, this rather surprising finding was replicated in a better controlled experiment. The essential difference between this study and the aforementioned McCoy & Jankovich experiment involved the level at which the experimental animals were chronically centrifuged.

In the latter experiment, rats were chronically centrifuged at 2.0 g, the upper limit of the spiral centrifuge employed in testing. All other features of the experiment remained unchanged. Results of this second experiment confirmed the McCoy & Jankovich findings. An initial but relatively weaker preference for 2.0 g was later replaced by a 1.0 g preference.

A second portion of this experiment involved animals chronically exposed to 1.5 g. When given a preference test, the animals spent the initial test sessions in the middle of the spiral test centrifuge; i.e., at 1.5 g. This initial preference also washed out and was replaced by a 1.0 g preference.

The above-described studies demonstrate clearly that gravity preference is both modifiable, and a function of the magnitude of pre-test gravity exposure. The subsequent preferences for 1.0 g found in virtually all chronically centrifuged rats is both interesting and puzzling. Could such a preference be modified in a permanent way? One possible approach to this alternative was attempted late in the grant period.

The basic rationale was to effect a permanent change in gravity preference produced by having animals spend virtually their entire lives in a gravity field in excess of 1.0 g. Toward this end, rats were to be conceived and born aboard a chronic centrifuge. After several problems with breeding and maintenance were worked out, the first litter of rat pups was born late in the grant period. At six months of age, they were given gravity preference tests in the special centrifuge. Again, the initial preference for high gravity environments was observed. However, a subsequent preference for low (1.0 g) gravity environments began to appear late in testing. Thus, it appeared that a preference for low gravity would override the background gravity environment.

III. Escape and Avoidance of High Gravity Environments

Numerous experiments have demonstrated that hypergravity is an aversive stimulus (Martin, Richardson, & Martin, 1966; Clark, Lange & Belleville, 1966; Clark, Lange, & Belleville, 1973). In each of these experiments, squirrel monkeys or rats were placed in a centrifuged capsule and trained to escape and avoid programmed increases in artificial gravity. Responses (usually lever presses) reduced centrifugally generated artificial gravity or postponed scheduled increases. The fact that virtually all experimental animals learned to produce the instrumental response is taken to indicate that hypergravity is indeed an aversive stimulus.

The above finding - that hypergravity is aversive - has been postulated as an explanation of gravity preference: That is, the escape and avoidance of gravity above 1.0 g may be the mechanism underlying the preference for 1.0 g.

During the current grant period two approaches were taken to explore the relationship between high gravity exposure and escape-avoidance responding. In the first paradigm, the relationship between avoidance and preference was explored from a correlational standpoint. Normally reared earth rats were given standard escape-avoidance training in a fixed-radius, variable speed centrifuge on Monday, Wednesday, and Friday of each week. On alternate days (Tuesday, Thursday, & Saturday) the animals received gravity preference tests in a spiral centrifuge. In both cases the gravity ranges were from 1.1 g to 2.1 g. Both preference and avoidance sessions were one hour in duration. Correlations were computed for performances in the two situations, i.e., number of avoidance responses and amount of time spent at 1.1 g in the preference tests. Correlation coefficients were extremely high, ranging from .97 to .88. An additional finding was that after a number of sessions (when both

preference and avoidance behaviors had stabilized) both measures began to show concomitant decreases. Thus, when the avoidance responding began to diminish, so did amount of time spent at 1.1 g in the gravity preference tests. Again the correlation was extremely high for all subjects. The observation that both avoidance and preference behaviors "go out" with prolonged training has been a common finding in this laboratory. The explanation is not immediately clear, however, some sort of adaptation mechanism has been postulated (e.g., McCoy, 1976).

A second, and more direct, tact was taken late in the grant period. The rationale underlying this approach is as follows: If gravity avoidance is the mechanism underlying gravity preference, then manipulations that affect one of these behaviors should also (and similarly) affect the other. Section II (Gravity Preference) demonstrated that chronic centrifugation could, temporarily, eliminate the preference for 1.0 g. What effect would chronic centrifugation have on avoidance behavior? Would an animal with a history of chronic exposure to high gravity now demonstrate an actual avoidance of low gravity fields?

Eight rats were chronically centrifuged for 6 months at 2.0 g. Eight control subjects were chronically centrifuged for the same duration, but over the axis of rotation. The controls, therefore, were exposed to the rotational forces, but not the g forces which the experimental subjects experienced. Half of the animals from each group received the standard gravity avoidance procedure wherein lever presses reduced gravity from 2.1 g to 1.1 g. For the remaining subjects, the avoidance training was reversed; i.e., lever presses produced high gravity and therefore, avoided low gravity.

As indicated previously, this project was initiated late in the grant period. It was plagued with personnel problems and technical malfunctions. Nevertheless, some trends were in evidence at the time that funding was terminated.

The chronically centrifuged animals did show a trend in the predicted direction. That is, more animals avoided 1.0 g than 2.0 g. This relationship was exactly the reverse for the control subjects; all avoided 2.0 g and none worked to avoid 1.0 g.

IV. Discrimination and Generalization of Gravity Stimuli

If gravity stimuli contain aversive properties, it also seems likely that they may exert other sorts of control over behavior. One such possibility is that gravity stimuli may exhibit discriminative properties. It was the exploration and delineation of such possibilities that constituted the major portion of the research conducted under this grant.

The prototype experiment was conducted by McCoy and Lange (1969). In two experiments, squirrel monkeys were exposed to centrifugally generated artificial gravity and trained to respond for food reinforcement at selected g levels. Experiment I involved single stimulus training in which a selected g level was chosen as the S+. In Experiment II subjects received discrimination training over two or three g values. The major findings were as follows: (1) Single stimulus training yielded linear relationships between percent of responding and magnitude of artificial gravity. (2) Two-valued discrimination training produced phenomena typically reported with other, more conventional, sensory modalities; viz behavioral contrast, and gradient peaks which were shifted from S+ in a direction away from S-. This effect was cancelled when S+ was located equidistant between two S- stimuli. (3) Gradient

form was independent of the $S^+ - S^-$ difference, but related to continuum location and/or intensity of the discriminative stimuli.

While the above-described experiment clearly demonstrates that gravity stimuli can function in the control of behavior as do other stimuli, interpretative problems arose from the fact that the McCoy & Lange experiments were conducted on a fixed-radius centrifuge. Thus, gravity changes were accomplished by changing angular velocity, which, in effect, confounded these two variables. Therefore, it was unclear which of the factors, angular velocity or resultant force (g) was controlling the behavior.

In order to understand fully the significance of the next experiment (which sought to alleviate this confounding), it is first necessary to examine the mechanics of artificially produced gravity. Gravity in excess of 1.0 g can only be produced in the earth-based laboratory by means of centrifugation. In this connection, rotation is an artifact which accompanies all such experiments. During rotation of a constant angular velocity (W) and at a constant radius (r) a mass (the experimental subject) is acted upon by the vector sum (a) of earth gravity and centrifugal acceleration, W^2r . This vector sum is frequently referred to as "artificial gravity", and it is conveniently expressed in units of g . Thus, if centrifugation produces a resultant acceleration of $a = 2.0 g$, the subject effectively weighs twice as much as it normally does at the earth's surface. Because earth gravity is fixed and centrifugal acceleration (W^2r) is a function of two variables (angular velocity and radius) differences in resultant acceleration (g) can be imposed on a subject in two ways, by changing angular velocity (as was done in the McCoy & Lange experiments) or by holding angular velocity constant and changing radius.

The next series of experiments attempted to separate angular velocity and resultant gravity by holding the former constant and varying radius of rotation. If it could be shown that such manipulations produce results equivalent to those described by McCoy & Lange, then it could be maintained that the principal variable involved in all of these experiments was, in fact, artificial gravity and not rotation.

McCoy, Love, & Miller (1972) conducted two such experiments. The first study employed squirrel monkeys which were initially trained and tested in a centrifuge capsule located 62.5 in. from the axis of rotation. In this capsule, the animals were trained to lever press for food at an S+ of 1.6 g (26.0 rpm). Next they were placed on discrimination training by extinguishing responding at chosen S- locations of 1.1 g and 2.1 g. They were then given a generalization test (in extinction) over seven test stimuli (1.1 g, 1.3 g, 1.5 g, 1.6 g, 1.7 g, 1.9 g, 2.1 g). Following the test, the animals were retrained on the 1.6 g - 1.1 g, 2.1 g, discrimination, still in the longer radius, 62.5 in. capsule. When responding had again stabilized, they were given a second generalization test, this time in a shorter radius (49.0 in.) capsule. The angular velocities associated with each of the original stimulus values of Test I were again provided in Test II, but since the Test II capsule was positioned at a shorter radius, the resultant gravities associated with each angular velocity were always less. The major finding of the experiment appeared in Test II where the animals showed maximal responding to the 1.6 g stimulus despite the fact that it was now produced by a much higher angular velocity. Had angular velocity per se been the primary stimulus controlling the behavior, gradient peaks would have occurred at 26.0 rpm in both Test I and II. This result clearly indicates that artificial gravity, and not rotation, was the controlling factor.

In a second experiment McCoy et al. explored the generality of the previous findings by employing a different species of subject (rats) and a modified test procedure. In this experiment, no explicit discrimination training was administered, and angular velocity remained constant throughout training and testing. All rats were trained to respond for food in cylinders positioned 22.5 in. from the axis of rotation. At a speed of 27.0 rpm a resultant force of 1.1 g was produced. During the generalization test, rats were assigned to one of six cylinder stations positioned from 78.0 to 22.5 (S+) inches from the axis of rotation. At a speed of 27.0 rpm, these test stations produced 1.9 g, 1.7 g, 1.5 g, 1.3 g & 1.1 g. Again, gradients revealed that maximum responding occurred at the 1.1 location. Responding decreased systematically as test stimuli departed from training stimuli, and orderly gradients were produced.

Taken together, these experiments demonstrate clearly that when artificial gravity and rotation are separated experimentally, the controlling stimulus is, in fact, gravity and not rotation.

A final project which was conducted during the grant period attempted to explore the effects of stimulus test order on pre- and post-discrimination gravity generalization gradients (Miller & McCoy, 1976). Three groups of squirrel monkeys received training and generalization testing on a constant-radius, variable speed centrifuge. Gravity was changed by varying rotational speed to determine the effect of test order on pre-and post-discrimination generalization gradients. Experiments I and II involved S+ - only training. Three separate orders of stimulus presentation (1.1 g - 2.1 g) were given in the generalization tests; ascending, descending, and random.

The first stimulus generalization gradients were non-horizontal and peaked above S+ for all stimulus orders. During the second generalization

test, all groups received both ascending and descending stimulus orders. Relative to the first generalization test, the second gradients revealed an increase on stimulus control for all subjects.

Gradients from both the first and second generalization tests displayed strong order effects. Relative to the ascending and random gradients, the descending gradients were shifted towards the high g regions.

In Experiment III successive discrimination training ($S^+ = 1.5$ g; $S^- = 1.9$ g) with ascending, descending and random test procedures produced typical post-discrimination gradients characterized by peak shifts and/or area shifts. The ascending gradients showed enhanced post-discrimination effects relative to the other orders.

These studies offer support for the contention that strong stimulus control is a necessary prerequisite for stable order effects.

V. Summary and Conclusions

The studies conducted under this grant focused upon the experimental analysis of the effects of gravity per se as a stimulus in the control of behavior. As such, this work is to be contrasted with numerous studies which view gravity as an interference factor as it relates to on-going behavior. The basic rationale continues to support the proposition that a thorough analysis of the effects of gravity should examine the fundamental role of this variable in the control of behavior.

The major findings of this research are as follows:

- (1) Strong gravity preferences for 1.0 g can be reliably demonstrated in several species of normally-reared earth animals. Such preferences are subject to modification providing that the "background gravity environment" is other than 1.0 g.
- (2) Gravity preference and the escape-avoidance of high gravity environments are highly related. These too, are subject to modification by high gravity "background stimuli". The proposed mechanism underlying both gravity preference and escape-avoidance is one of adaptation.
- (3) Gravity stimuli exert discriminative control over behavior. It has been demonstrated through discrimination-generalization procedures that gravity stimuli can control behavior in a manner similar to other, more conventional, stimulus dimensions.

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